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A PROPOSED DUAL ROLE OF ODOR IN FORAGING BY THE CALIFORNIA SPINY LOBSTER, *PANULIRUS INTERRUPTUS* (RANDALL)

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Abstract

A dual influence of odor on foraging is proposed for *Panulirus interruptus,* on the basis of laboratory and field tests using abalone muscle effluence as a stimulant. Food search consisted of three major components: detection (increased antennule flicking), locomotion, and non-locomotor probing by pereiopod dactyls. Detection occurred at lower concentrations (10^{-8} to 10^{-10} g/l) and was initiated before probing and locomotion in laboratory tests. Probing occurred at concentrations $\geq 10^{-6}$ g/l and was initiated before locomotion. Locomotion was limited to higher concentrations ($\geq 10^{-4}$ g/l) and its induction frequently followed introduction of an effective chemical stimulus by 60 s or longer. The response hierarchy in *Panulirus* indicates that concentrated chemical stimuli may initiate only local searches for food.

Traps were baited with abalone muscle for field experiments. Effective effluent concentrations in immediate trap environments were estimated by a three-dimensional Fickian diffusion model. The minimum concentration attracting lobsters was estimated to be nearly identical to the laboratory-determined threshold for detection, 4–6 log units lower than the threshold for induction of locomotion. Lobsters were captured in traps primarily at night, the period of greatest normal, endogenously initiated activity. Consequently, low concentrations may act by modifying behavior of animals already aroused, rather than by initiating foraging or feeding from the quiescent state.

Introduction

Chemical stimuli induce food search in decapod crustacea frequently in the absence of other sensory cues (McLeese, 1970, 1973a; Shelton and Mackie, 1971; Mackie and Shelton, 1972; Mackie, 1973; Carr and Gurin, 1975; Hindley, 1975). Laboratory experiments have shown visual and tactile prey stimuli often are without effect, while odors released from prey cause marked food searching responses (Derby and Atema, 1981; Schembri, 1981; Zimmer-Faust and Case, 1982a). Field experiments have recently demonstrated that the lobster, *Panulirus interruptus,* and the crabs, *Cancer antennarius* and *Loxorhyncus grandis,* discriminate among odors of adjacently positioned foods and that chemical stimuli direct the movements of lobsters both towards and away from potential food items (Zimmer-Faust and Case, 1982b).

Chemical stimuli are commonly believed to influence decapod foraging by triggering distance chemoreception (Hazlett, 1971a, b; McLeese, 1973b; Ache *et al.,*

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1978; Pearson *et al.,* 1979; Reeder and Ache, 1980). According to this model, dilute attractant concentrations are thought to stimulate highly sensitive chemoreceptors, thus causing locomotor responses towards distant targets. Chemical concentration is assumed to be an important cue relating distance to food, and dilute attractant concentrations are presumed to be interpreted by animals as originating from distant food sources. Highly sensitive chemoreceptors have been identified on the antennules of the Florida spiny lobster, *Panulirus argus* (Fuzessery, 1978; Thompson and Ache, 1980), and extremely low behavioral thresholds for detection have been observed in other decapods (Pearson and Olla, 1977; Price and Ache, 1977; Pearson *et al.,* 1979); however, it has yet to be demonstrated that very low stimulant concentrations can induce locomotion. Decapods are presently known to initiate locomotion at concentrations of 10^{-6} to $\geq 10^{-2}$ g/l, when responding to various tissue extracts (Mackie and Shelton, 1972; Mackie, 1973; McLeese, 1973a; Pearson *et al.,* 1979). Orientation to chemical gradients has been demonstrated for the lobsters, *Homarus americanus* and *Panulirus argus,* but exclusively in response to extract concentrations $\geq 10^{-3}$ g/l (McLeese, 1973b; Reeder and Ache, 1980). These results suggest that chemical stimuli influence local searches for food, where high stimulant concentrations are maintained, but offer little evidence concerning the effect of chemical stimuli on distant foraging.

The present study was conducted to determine the influence of odor on foraging behavior of the California spiny lobster, *Panulirus interruptus* (Randall). Laboratory and field estimates were made for concentrations of effluence released from abalone (*Haliotis* spp.) muscle that would be effective in stimulating lobsters. Results showed that high concentrations initiated behavioral patterns of local searches for food. Low concentrations appeared to modify, but not initiate, distant searches for food. Evidence showed that the action of chemical stimuli was limited to the near vicinities of food, and that long-range chemosensory responses were unlikely to be manifested by *Panulirus* in its naturally turbulent habitat.

Materials and Methods

Selection of abalone muscle effluence as chemical stimulant

In the selection of a chemical stimulant for this investigation, it was essential that it be capable of inducing food search in lobsters under both laboratory and field conditions. Ideally, this stimulant should consist of one or only a few readily detectable compounds. Low molecular weight substances, particularly amino and organic acids, were desirable constituents for the stimulant because standard chemical assays exist for these compounds, and laboratory studies show amino and organic acids to be highly effective in stimulating food search among decapod crustacea (McLeese, 1970; Shelton and Mackie, 1971; Mackie, 1973; Hindley, 1975; Carr, 1978). Unfortunately, release of single amino and organic acids has failed to attract animals consistently in field experiments (Allen *et al.,* 1975; Ache *et al.,* 1978).

Preliminary to the present investigation, we performed tests involving release of single amino and organic acids and a five-component amino-organic acid mixture from polyacrylamide gels. These solutions failed to attract lobsters, as in previous studies, even though they were highly stimulatory in laboratory tests. Gels releasing a sea water extract of abalone muscle successfully attracted lobsters. Effluence from abalone muscle was, therefore, selected for use in present experiments. While not providing a completely defined chemical stimulus, abalone muscle produces an attracting odor in both laboratory and field experiments (Zimmer-Faust and Michel, 1980; Zimmer-Faust and Case, 1982b). Abalone muscle is available to *Panulirus*

as carrion in the natural habitat. Stimulatory molecules released by abalone muscle are identified as peptides and polypeptides of widely ranging molecular weights (Zimmer-Faust and Michel, 1980).

Laboratory experiments: collection and maintenance of animals

Lobsters were captured by hand (SCUBA) or by trap at More Mesa reef, the habitat used for our field trapping experiments, 4 km east of the U.C. Santa Barbara campus. Captured animals were brought immediately to the laboratory and held in groups of 10 individuals in 3,000 l aquaria, for 10–14 days prior to experiments. Excess shelters were provided. A continuous, single-pass sea water flow (5 μm filtered) in each holding tank maintained aeration and ambient sea temperatures (16–19°C). All incoming animals were marked using the tattoo method of Kuris (1971), and carapace length, sex, and reproductive status were recorded for each animal. Only adult intermoult animals of mean carapace length, 66 mm ($\pm$3 SD), were used in experiments. A 12:12 D:L cycle (light on: 0600–1800 h) was maintained throughout holding and experimental periods, and all tests were conducted during the 1900–2400 h period. Animals were fed abalone muscle, mackerel muscle, and opened mussels *ad libitum* on alternate days and deprived of food for 24 h before testing.

Test apparatus

Animals were individually tested for responses to chemical solutions in rectangular aquaria, $30 \times 30 \times 13$ cm constructed so as to allow precise control of stimulus flow characteristics. Opaque blinds around each aquarium allowed observation without disturbing test animals. Dim lighting was provided by 25-watt red incandescent bulbs in diffusing housings placed 50 cm above aquaria. Lighting was completely confined by the blinds and the surrounding laboratory was maintained in darkness to reduce disturbances to test animals. Responses of animals in these experiments were nearly identical to those of animals tested later, both during the day and at night, using ambient light intensities measured at the collection site (T. Frank, Dept. of Biology, U.C. Santa Barbara, pers. comm.). Light intensities used in present experiments, therefore, appear not to influence behavioral thresholds.

Sea water entered each test aquarium by a delivery system maintained under constant hydrostatic pressure. Polyethylene tubing carried a primary sea water flow (980 ml/min) from a head-tank to a Nalgene adapter, where it was then delivered to each test aquarium at the centerpoint, 0.5 cm below the water surface. A valve in each delivery tube enabled fine adjustments of water flow. A secondary flow to each aquarium, serving as a loop injector for stimulants, was carried by polyethylene tubing (120 ml/min) from a head-tank to a stimulus reservoir, before it joined with the primary flow at a Nalgene adapter. Stimulant was introduced (10 ml/7 s) by opening a three-way valve that connected the stimulus reservoir to the secondary flow system, and flow was uninterrupted during stimulant introductions. A fitting in each Nalgene adapter eliminated back-pressure on secondary flow, causing sea water and stimulants to pass from secondary to primary flow before entering aquaria.

Fluorescein dye (10 ml/7 s) was used to estimate stimulus dilutions. A Masterflex peristaltic pump (Model 7568) coupled to 1.57 mm ID polyethylene tubing continuously evacuated sea water from experimental aquaria (2 ml/min), beginning 180 s prior to and continuing for 180 s following an introduction of dye. Evacuated water was continuously pumped through a Turner fluorometer (Model 111) having Whatman 2A and 47B excitation filters and a Whatman 2A-12 emission filter. Fluorometer output was recorded on a chart recorder. Standards were prepared

from fluorescein dye and calibration curves were generated using the fluorometer. Two dye injections were performed for each aquarium, while assay water was evacuated from tubing attached to the basal segments of antennules of unrestrained lobsters. Dye tests indicated that stimulant delivery and mixing was uniform among the test aquaria.

Preparation of test solutions

Stimulants were prepared by collecting abalone muscle effluence (AME) from tissues as they were readied for field experiments. To standardize chemical composition, only one collection was made from which all stimulants were produced. Following collection, AME was filtered (Millepore 0.45 μm membrane) and vortex-stirred to produce a homogeneous mixture. Aliquots of 1 ml were placed in test tubes, capped, and frozen.

Stimulant concentrations were determined by removing fluids (AME) from randomly selected test tubes and heating at 40°C until stable dry weights were attained. Concentrations were determined as the mean dry weight of material (g) per fluid volume AME (ml). These procedures controlled for possible discontinuities in the collection and subsampling of AME. Aliquots were considered homogeneous if nearly identical dry weights were attained for each sample.

Test procedures and threshold determinations

Testing consisted of a random presentation of a test or control stimulus to an animal in a randomly selected aquarium. Animals were actually tested only if inactive, so that procedures would conform to those of previous investigations (*e.g.* McLeese, 1970; Mackie and Shelton, 1972; Mackie, 1973; Pearson and Olla, 1977; Ache *et al.*, 1978; Pearson *et al.*, 1979; Derby and Atema, 1981). Identical solutions were never repetitively introduced to the same animal during the experiment. Only one trial was performed per animal on any single day. At the conclusion of the experiment, each of the 6 different test and control stimulants had been introduced to the same 25 animals.

All trials were conducted by one person who did not know the composition of solutions being tested. Animals were put in experimental aquaria 90–120 min prior to testing and settled within 30–40 min. Observations of behavior were initiated 1 min before stimulus introduction and continued for 3 min after introduction. Verbal descriptions were recorded using a portable tape recorder and were later transcribed and analyzed. Movements associated with locomotion and with non-locomotor probing by pereiopod dactyls were selected for observation because of their obvious roles in searching for distant and local food items, respectively. Antennule flicking was also observed because electrophysiological and behavioral experiments show increased rates of flicking commonly associated with the detection of chemical stimuli (Snow, 1973; Pearson and Olla, 1977; Price and Ache, 1977; Pearson *et al.*, 1979; Schmitt and Ache, 1979). Threshold concentration for each component behavior was defined as the lowest tested concentration to which the proportion of responding animals was significantly greater ($P < 0.05$) than the proportion responding to filtered sea water. Significance levels were determined using the Fisher Exact Test.

Field experiments: general procedures

Tests were performed to estimate concentrations of abalone muscle effluence in the immediate vicinities of traps capable of attracting lobsters. All experiments

were conducted at More Mesa reef, where 8 stations were permanently buoyed in 2–4 m water depth. Each station was separated by a minimum of 15 m. Elliptically shaped polyethylene mesh traps were used, 100 cm × 79 cm × 30.5 cm (Fathoms Plus, San Diego, CA). Since repetitive trapping was conducted at a restricted number of sites, the possibility of immediate recapture and trap habituation existed. To monitor this possibility, captured animals were tagged with return addressed, serially numbered anchor tab tags. All tagged animals were released at the point of capture.

Comparisons among capture rates of lobsters are more rigorous if water conditions are known. For this reason, we used the dissolution rate of cast calcium sulfate blocks as a general measure of wave and surge conditions (Doty and Doty, 1973). Twenty-five g cubes were formulated as described by Zimmer-Faust and Case (1982b). On each test date, 8–16 cubes were placed in labeled Vexar bags (0.32 cm mesh) and exposed both in field and laboratory for 24 h. In the field, cubes were placed in a trap having closed entries, located at the centerpoint of the trap matrix. In the laboratory, each cube was placed in a separate 12 l sea water bath without water motion and held at ambient sea temperature. A relative water motion index was created. An index value of zero indicated that the dissolution rate of field-placed cubes was equal to that of cubes positioned in water baths and that no water motion had occurred (Zimmer-Faust and Case, 1982b). A value of one meant that field cubes had totally dissolved. Index values of zero and one were never attained.

Preparation of tissues

Prior to field use, abalone muscle was chopped in a Furnas Buffalo Chopper (Model JP 5) at low speed for 30–60 s and reduced to 1–2 cm cubes. Chopping was deemed essential to increase tissue surface area exposed to sea water and thus to improve the catch. Lobsters were previously found unattracted to live-prey baited traps (Zimmer-Faust and Case, 1982b). Immediately following chopping, tissue was flash frozen at −70°C. Twenty-four hours prior to use the bait was thawed to 0°C and apportioned into labeled 0.32 cm mesh Vexar bags. Rittschof (1980) has shown action of freeze-thawing on chopped molluscan tissues to be similar to that of natural autolytic degradation. Tissue-filled bait bags were placed in a 2.5 cm mesh Vexar box, removed to a temperature-humidity controlled room (temp: 10°C; rel hum: 50%) and allowed to thaw for an additional 12 h. Wet weights were determined and tissues were immediately used in trapping. Effluence was collected as thawing occurred, and used as the stimulant in present laboratory experiments. Vexar bags provided a precise means of placement and later removal of specified amounts of tissues from traps. Bags were inaccessable to captured animals, guaranteeing that only waterborne substances were available as chemical cues.

Test procedures

Seven different quantities of abalone muscle, from 3–372 g, were tested for effectiveness in capturing lobsters. Within any two-day period a single quantity of abalone was tested against empty Vexar packets, using bait reversal procedures (Zimmer-Faust and Case, 1982b). At each of the 8 stations, two traps were paired 1–2 m apart. On the first day, tissue was placed in one trap while an empty Vexar packet was placed in the alternative trap. The first day allocation of tissue was at random and traps were raised after 24 h. On the second day, traps were identically placed with bait positions reversed.

Tests were conducted for a total of 14 two-day periods. During the initial seven two-day periods, abalone mass was successively halved and presented in a descending

order. In the final seven two-day periods, quantities of abalone were tested in a randomized order. Data were initially analyzed using Wilcoxon paired comparison tests. In the present report, data were summarized as the total number of animals captured per bait treatment, and exclusive use was made of Chi-square tests for heterogeneity. Significance levels determined by Chi-square were identical to those determined by Wilcoxon.

Rates of effluence

Tissues were placed in traps closed to entry and positioned in the study area during field trapping experiments. Wet weights were determined for these tissues before and after removal from traps, following 0, 1, 2, 4, 8, 18 or 24 h. Dry weights were subsequently determined and wet weight-dry weight regressions were generated for tissues not field exposed. This enabled calculation of both wet and dry weight losses for field-exposed tissues. Field exposure durations were carefully recorded to the minute, and rates were determined as derivatives relating the instantaneous reduction in bait mass to field exposure duration. Rates were later used to estimate effluence concentrations in immediate trap environments since direct assay was impossible.

Results

Laboratory experiments

Peak concentrations of dye attained in test aquaria were 1.02×10^{-3} ($\pm 0.13 \times 10^{-3}$ SD) times original injected concentrations. Peaks occurred 19 s (± 4 SD) after

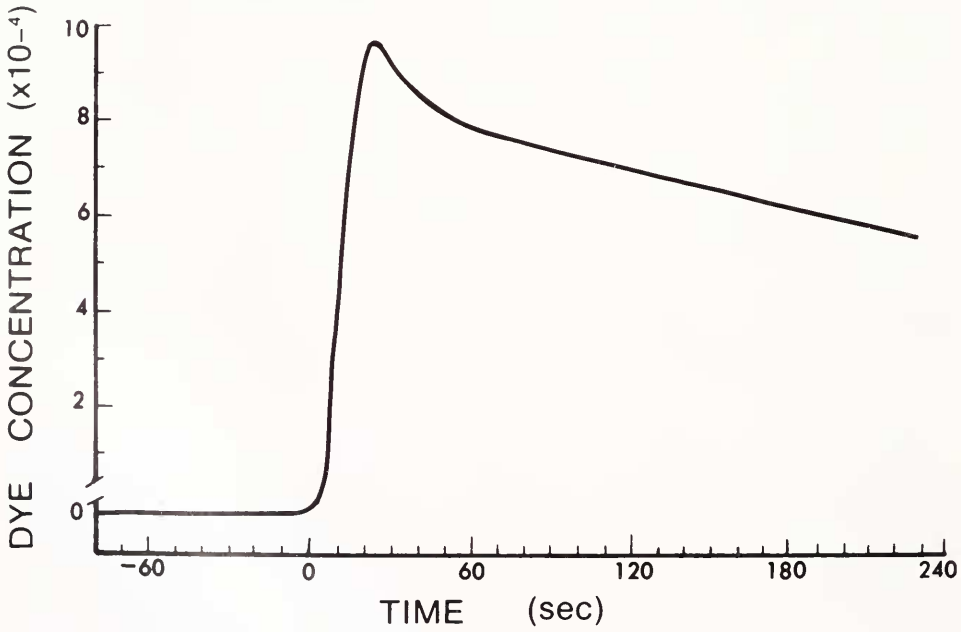

FIGURE 1. A record showing the flow characteristics of a test aquarium following dye introduction (10 ml/7 s). The maximum concentration achieved is 9.7×10^{-4} times the original injected concentration. Time equals zero is defined as the initiation of dye input. Water was evacuated (2 ml/min) from tubing attached to the basal segments of antennules of lobsters, and dye concentrations were continuously monitored using a fluorometer.

TABLE I

Initiation of behavior following stimulus introduction[a]

Behavioral component	Time of initiation (s)[b]	Ranked order of initiation		
	Median (range)	First	Second	Third
Detection (increased antennule flicking)	2(1–15)	19	7	0
Probing	3(2–121)	7	18	1
Locomotion	45(10–176)	0	1	25

[a] Includes only those 26 trials in which all 3 behavioral components were observed.
[b] Time equals zero defined as initial stimulus input.

initial dye input and decayed to 68% of maximum within the 180 s observation period (Fig. 1). Flow characteristics were nearly identical for each experimental aquarium, with no significant differences occurring among peak concentrations, latencies, or decays (One-way ANOVA, with replicates: d.f. = 7/8, $F \leq 1.89$, $P \gg 0.10$, all comparisons).

Concentrations of sampled AME aliquots were equivalent and ranged from 9.80×10^{-2} to 9.89×10^{-2} g/ml, with a mean of 9.83×10^{-2} g/ml ($\pm 0.03 \times 10^{-2}$ SD). This indicated that the collection and subsampling of AME was homogeneous. Average concentrations of AME, in contact with test animals were calculated by multiplying 9.83×10^{-2} g/ml times serial dilutions (10^{-1}, 10^{-3}, 10^{-5}, 10^{-7} and 10^{-9}), then multiplying again by the mean stimulus dilution (1.02×10^{-3}). This gave average concentrations contacting the animals of 1.00×10^{-2}, 10^{-4}, 10^{-6}, 10^{-8} and 10^{-10} g/l. Hereafter, concentrations cited are those contacting animals.

Response hierarchy

The behavioral components of food search were exhibited in a linear hierarchy. Increased antennule flicking and probing of legs occurred immediately upon the introduction of an effective chemical stimulus, while locomotion was often delayed for 60 s or longer (Table I). When all three behavioral components were observed in the same trial, flicking was initiated before leg probing, which in turn nearly always preceded locomotion. Threshold concentrations for antennule flicking, leg probing, and locomotion were 10^{-8}, 10^{-6}, and 10^{-4} g/l, respectively (Table II). Thresholds appeared representative for leg probing and locomotion, but a large proportion of animals responded to 10^{-10} g/l by increasing antennule flicking. Consequently, a threshold of 10^{-8} to 10^{-10} g/l seems probable for this behavior.

Field experiments

Recapture rates were low for *Panulirus* during field experiments. Only 2.1% of all tagged animals were recaptured. Lobsters recaptured during ensuing commercial seasons increased the total recapture to 10%. This indicated that tags were successfully retained by lobsters, and that near non-replicate capture occurred in our experiments.

Traps having 46–372 g abalone were equally effective in capturing lobsters, while a significant decrease in capture occurred with less than 20 g abalone per trap (Table III). Quantities as low as 7.20 g/trap were effective in capturing animals. Abalone mass decreased linearly as a function of field exposure duration over the first 24 h,

TABLE II

Number of animals responding to stimulants

Concentration (gm/l)	Behavioral component: Detection (Increased antennule flicking)	Probing	Locomotion	Sample size
10^{-2}	25***	23***	16***	25
10^{-4}	25***	14*	6*	25
10^{-6}	20**	13*	2	25
10^{-8}	24***	9	3	25
10^{-10}	16	5	1	25
0 (Sea water controls)	10	6	0	25

* The difference between the proportion of animals responding to test as opposed to control solutions is significant (Fisher Exact Test: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$).

meaning that the rate of effluence was constant for this period (Table IV). A sigmoidal log-linear relationship was observed between capture efficiency and rate of effluence, and rates differing less than one log unit in magnitude caused widely varied captures (Fig. 2). This indicated that effluent releases, hence the effluent concentrations in immediate trap environments, were critical in the attraction of lobsters. Effluences of 0.04 g/h caught low but significant numbers of lobsters, while effluences of ≥0.32 g/h produced maximum asymptotic capture rates.

The possibility existed in field experiments that microbial action influenced the stimulatory capacity of abalone muscle, making field and laboratory stimulants not comparable. To explore this possibility, we prepared an extract from lyophilized

TABLE III

Lobsters captured in trapping experiments using abalone muscle as bait

Initial mass[a] (g wet weight) $\bar{x} \pm se$	(abalone-baited vs unbaited traps)[b]: Day 1	Day 2	Day 3	Day 4	Total	Rate of effluence (g/h): Wet weight $\bar{x} \pm se$	Dry weight $\bar{x} \pm se$	Water flow[c] index values $\bar{x} \pm se$
372 ± 6	15–2	21–0	19–0	22–3	77–5***	3.8 ± 0.3	0.9 ± 0.1	0.53 ± 0.02
176 ± 4	11–0	13–1	30–2	16–1	70–4***	1.3 ± 0.3	0.32 ± 0.08	0.55 ± 0.04
93.96 ± 2.29	41–1	23–0	7–0	16–0	87–1***	0.93 ± 0.12	0.20 ± 0.02	0.56 ± 0.02
46.71 ± 0.45	6–2	23–2	27–0	23–1	79–5***	0.32 ± 0.05	0.07 ± 0.01	0.51 ± 0.01
18.44 ± 0.16	17–3	13–1	7–0	10–0	47–4***	0.06 ± 0.02	0.01 ± 0.005	0.56 ± 0.01
7.20 ± 0.12	4–4	9–3	8–1	0–1	21–9*	0.04 ± 0.01	0.009 ± 0.002	0.51 ± 0.01
2.61 ± 0.06	0–0	1–3	1–1	2–1	4–5	0.015 ± 0.004	0.004 ± 0.001	0.58 ± 0.04

[a] g dry weight = 0.23 (g wet weight) + 0.07 (Product moment correlation coefficient = 0.99 ± 0.01 se; n = 25).

[b] The number of lobsters captured in abalone-baited traps is underlined.

[c] Differences between water flow index values are not significant (One-way ANOVA, with replicates, df = 6/21, F = 1.55, $P > 0.10$).

* The difference between the total number captured in abalone-baited *vs* unbaited traps is significant (Chi-square test for heterogeneity: df = 1, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$).

TABLE IV

Regression equations describing abalone effluence

Initial mass (g wet weight)	Equation[a]	Correlation coeff. (R ± se)	F test d.f.	F test Value	F test *P*
372.	$A_t = A_0[1 - (0.01t + 0.05)]$	0.86 ± 0.06	1/12	34.20	<0.001
176.	$A_t = A_0[1 - (0.008t + 0.08)]$	0.84 ± 0.05	1/12	28.79	<0.001
93.96	$A_t = A_0[1 - (0.01t + 0.06)]$	0.91 ± 0.04	1/10	50.03	<0.001
46.71	$A_t = A_0[1 - (0.007t + 0.06)]$	0.87 ± 0.04	1/12	38.46	<0.001
18.44	$A_t = A_0[1 - (0.004t + 0.07)]$	0.54 ± 0.05	1/12	4.97	<0.05
7.20	$A_t = A_0[1 - (0.006t + 0.02)]$	0.64 ± 0.07	1/10	6.71	<0.05
2.61	$A_t = A_0[1 - (0.006t + 0.01)]$	0.65 ± 0.06	1/17	11.66	<0.005

[a] Predicted y-intercepts ($A_{t=0}$) closely approximate observed 1–8% mass losses incurred during transports of tissues to and from the field.

A_0: Initial mass before transport to the field; A_t: Final mass after transports and field exposures; t = 0: Field placement of abalone.

tissue using glass-distilled water, which we bound in polyacrylamide gel and used as bait. Control stimulants were identically prepared, except glass-distilled water was bound in gel without abalone muscle extract. Polyacrylamide gel is not susceptible to microbial decomposition and the small pore size prevents penetration by microbes (Allen *et al.*, 1975). Traps were paired at 8 stations with abalone gel (400 ml) placed

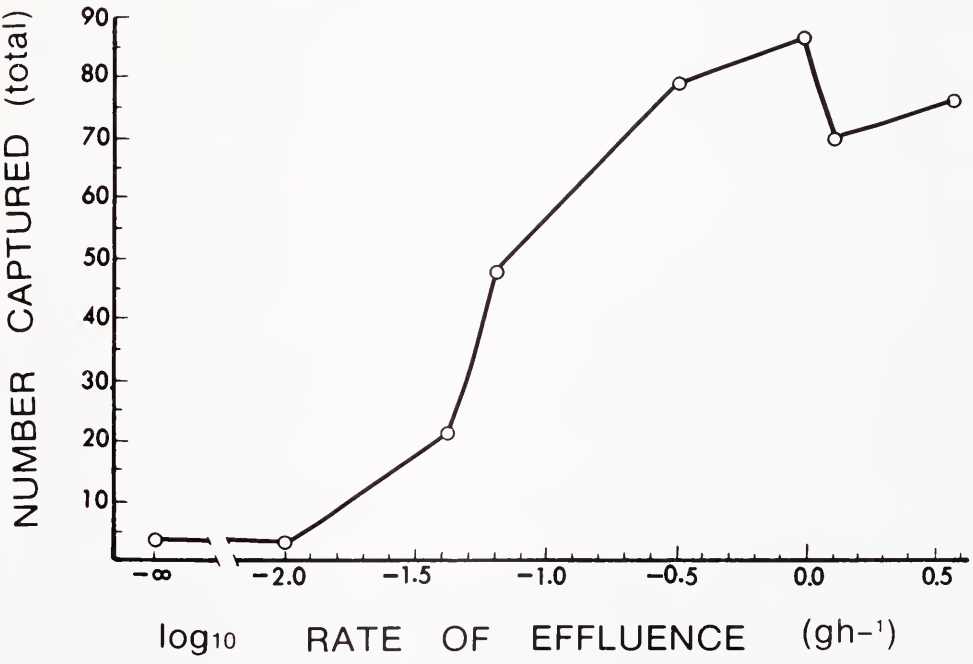

FIGURE 2. The log-linear relationship for captured lobsters, expressed as a function of the rate of abalone muscle effluence (wet weight). A log-linear dependence occurs over the −1.5 to −0.5 log unit interval. An effluence of negative infinity represents unbaited (control) traps, with the mean capture presented.

in one trap of each pair, while control gels were placed in alternative traps. Traps were raised each 24 h and gels were replaced and their positions reversed, for four consecutive days. Twenty-five lobsters were captured in traps having abalone gels, while only 6 lobsters were captured in traps having control gels, a significant difference (Chi-square test: $\chi^2 = 11.65$, d.f. = 1, $P < 0.001$). Abalone material lodged in gels was only 0.62 g/trap (dry weight) and the maximum amount of material released was 0.38 g trap^{-1} day^{-1}. This value compared favorably to the average total material released by 7.20 and 18.44 g abalone (0.22 and 0.33 g trap^{-1} day^{-1}, respectively). The number of lobsters captured in traps using abalone gels was also similar to the number captured in traps using 7.20 and 18.44 g abalone tissue (Table III), suggesting that the stimulatory capacity was nearly equal for effluence released by gels and by natural tissues. Microbial influences, therefore, appeared to be of minimal consequence in present experiments. Thresholds for locomotion (10^{-3} g/l) and for detection ($<10^{-7}$ g/l) were nearly identical in laboratory experiments using extract prepared from lyophilized tissues, as in experiments using AME (Zimmer-Faust *et al.*, unpub. data).

Discussion

Trapping experiments were conducted in turbulent waters adjacent to breaking surf causing strong oscillatory on- and off-shore surges (20–50 cm/s) to be maintained and superimposed on weak longshore currents. Inman *et al.* (1968, 1971), investigating dispersions of dyes in similar surf zone waters, found that dye diffused by turbulences according to Fick's Law, primarily in on- and off-shore directions. Dye was also transported advectively by longshore currents, but longshore dilution was nearly zero for weak currents. Based on these findings, we apply Fick's Law to present data and estimate effective concentrations of abalone muscle effluence in waters adjacent to traps. In applying Fick's Law, we assume a weak longshore current, isotropic turbulence, and an ocean floor impervious to the flow of stimulants. For these conditions, the mean effluent concentration (N) at position (x, y, z) and time, $t \geq 0$ is:

$$(1) \qquad N(x, y, z, t) = \frac{q(t)}{4(\pi D)} \frac{3}{2} \int_0^t \exp\left\{\frac{[x - U(t - t')]^2 - y^2 - z^2}{4D(t - t')}\right\} \frac{dt'}{t - t'}$$

where q(t) is the rate of effluence, D is a diffusivity constant and U is the longshore current velocity. Abalone muscle was positioned at space coordinates, $x = y = z = 0$, and $t = 0$ was defined as the time of initial abalone placement. The rate of effluence was both continuous and constant, and depended slightly on the initial mass of abalone (Table IV). When time becomes large, effluence concentration (N) in equation 1 approaches the limit:

$$(2) \qquad N(x, y, z, t) = \frac{q}{2\pi Dr} \exp\left[\frac{-U}{2D}(r - x)\right]$$

where r is the vector distance from abalone $(x^2 + y^2 + z^2)^{1/2}$. It can be assumed that time is large in present experiments, because lobsters initiated foraging at dusk, 7–10 h (28,000–36,000 s) after bait placement of abalone (Lindberg, 1955; Winget, 1968; Carlberg, 1975; unpubl. obs.). Maximum concentrations occurred at positions lying on the x-axis, in line with the longshore current, where $r = x$ and $\exp[-U(r - x)(2D)^{-1}] = 1$. For present calculations, diffusivity constants (D) were taken as 0.03–5.9 m^2/s from Inman *et al.* (1971), and the minimum effective concentration

was estimated by considering that 7.20 g abalone leached effluent at 0.04 g/h (10^{-5} g/s), yet attracted significant numbers of lobsters. For these conditions, effluent concentrations approached 3×10^{-7} to 2×10^{-9} g/l at trap perimeters, distances of only 17 cm from the abalone tissue source ($r = x = 0.17$ m). Concentrations become 6×10^{-8} to 4×10^{-10} g/l when converted to dry weight units. Asymptotic captures occurred when substances were leached at rates ≥ 0.32 g/h (Table III), producing concentrations $\geq 4 \times 10^{-7}$ to 5×10^{-9} g/l (dry weight). Diffusivity values were unlikely to cause error in present calculations, because values were taken for lower and higher turbulences than at our study site.

From the above calculations using natural tissues, two major findings appear: (1) Abalone muscle effluence evokes responses under field conditions at concentrations near laboratory-determined detection limits. *Panulirus* detected 10^{-8} to 10^{-10} g/l (dry weight) abalone muscle effluence (AME), as assayed by increased antennule flicking in laboratory experiments. Absolute thresholds for detection may be even lower. (2) Effective field concentrations of abalone muscle effluence were 4–6 log units more dilute than the laboratory-determined threshold for a chemical induction of locomotion. Lobsters initiated locomotion at concentrations $\geq 10^{-4}$ g/l AME, in laboratory tests. This high threshold for locomotion in *Panulirus* did not appear to be a laboratory artifact associated with tank construction, since other decapods tested in larger aquaria also initiate locomotion at similar concentrations, 2×10^{-6} to 3×10^{-5} g/l, when responding to various tissue extracts (Mackie and Shelton, 1972; Mackie, 1973; McLeese, 1973a; also see Pearson and Olla, 1977, for threshold estimates). This leads us to believe that chemical activation of distant foraging is unlikely in *Panulirus*. Chemical stimuli most likely initiate only local searches for food, where high stimulant concentrations are maintained. The insensitivity of the locomotor response and the preferential search with pereiopod dactyls were both adaptive for local but not for distant food searches.

Panulirus interruptus is known to locomote spontaneously at night (Lindberg, 1955; Winget, 1968; Krekorian *et al.*, 1974). Consequently, chemical induction of locomotion is unnecessary for distant foraging to occur. Based on our results, low concentrations appear to act by modulating, rather than by activating, distant locomotion patterns. This hypothesis is supported by our finding that baited traps captured lobsters nearly always at night, during the period of greatest endogenous activity (unpubl. data), whereas lobsters tested in the laboratory at night while inactive were found to be insensitive in their locomotor responses to chemical stimuli. It can always be argued that, in the laboratory, inability to dilute stimuli to effect lobster locomotor behavior results from laboratory-induced trauma. We admit this possibility, but feel the argument is unjustified since it can be applied indiscriminately to all laboratory investigations. Experiments are now needed to test responses of inactive and active animals held in large tanks simulating natural conditions. Even these experiments will not be without bias, however, since the natural flow dynamics of stimulants will not be reproduced.

We performed experiments using paired traps positioned 1–2 m apart, with bait tissues in one trap of each pair, leaving alternate traps empty. Initial bait placement was at random, and baits were replaced and their positions reversed from the first to the second day. Captures on consecutive days between paired traps with bait tissues of identical masses were compared, and in 4 out of the 8 trap stations, the number of lobsters captured in one trap was consistently greater than that of the alternate trap (Chi-square test: $P < 0.05$, 4 out of 8 comparisons). This means that the precise position of food is important in the attraction of lobsters and that at distances removed only 1–2 m from food, the influence of odor is greatly reduced.

Locomotion activated by stimuli not specifically related to a food source thus appears to be of vital importance, and the ability of lobsters to acquire food may depend on contacts with very limited chemically active spaces.

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